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Plant Associations and Primary Productivity of the Nisqually Salt Marsh on Southern Puget Sound, Washington

Abstract

A study of plant associations and primary productivity was conducted on the salt marsh of the Nisqually River delta located at the southern end of Puget Sound in the State of Washington, U.S.A. Vegetation was sampled along transects placed perpendicular to observed environmental gradients. Twelve plant associations were defined and a vegetation map was prepared showing their extent and location. The distribution of associations appears to be determined by the combined effects of elevation-inundation and the fresh water influence of the Nisqually River. Productivity values were estimated for eight associations using a clip-harvest method, with samples taken at monthly intervals. The average annual net productivity of these eight associations is 814 g dry weight/m^2 with a range of 90 to 1390 g dry weight/m^2. The *Festuca rubra-Carex lyngbyei* association is the most productive of the associations found at high elevations while the *Carex lyngbyei* association, found at low elevations, is the most productive of the associations sampled.

Introduction

Salt marshes are found along both the east and west coasts of North America. On the east coast, salt marsh ecology has been the subject of intensive research. Pomeroy (1959) estimated annual net productivity of benthic algae in Georgia salt marshes. Teal (1962) proposed an annual energy budget for a salt marsh ecosystem in Georgia. Spermatophyte net productivity values have been determined for marshes along the east coast by Steever (1972) and Odum and Fanning (1973).

Until recently, studies of salt marshes on the west coast of North America have been limited and mostly descriptive in nature. Purer (1942) described the vegetation of salt marsh ecosystems along the coast of southern California and discussed the anatomical adaptations of the various species to their environment. Hinde (1954) examined the relation between tidal inundation and distribution of salt marsh vegetation in San Francisco Bay. Macdonald and Barbour (1974) contributed a classification and description of major salt marsh floristic zones from the Aleutian Islands to Baja California. Jefferson (1974) defined plant communities, described their zonation, and investigated several environmental factors influencing plant succession on salt marshes of the Oregon coast. Eilers (1975) estimated net primary productivity of plant communities on a marsh in Nehalem Bay, Oregon, and described community zonation, productivity, and species diversity as they relate to elevation and inundation.

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Crow (1977) described the vegetation of some salt marshes of the Alaska Pacific coast and discussed environmental factors influencing the zonation of plant communities.

To our knowledge, no major studies have been published on salt marshes of the Washington coast. The purpose of our study was to define the plant associations on the salt marsh of the Nisqually River delta and to estimate the annual net primary productivity of these associations.

Study Area

Location. The delta of the Nisqually River is located in Thurston and Pierce Counties, Washington, 16 km northeast of Olympia, Washington (Fig. 1). The delta is a part of the estuary formed by the Nisqually River and McAllister Creek where they enter southern Puget Sound. This area includes salt marsh modified by diking, salt marsh periodically inundated by the tides, and sand-mudflats which extend north to Nisqually Reach. Our study was confined to the undiked salt marsh.

Climate. The Puget Sound area is characterized by a mild, maritime climate including prolonged cloudy periods, narrow diurnal temperature fluctuations, and a long frost-free season. Winters are mild; summers are cool and relatively dry. January mean minimum temperature in Olympia is –0.5°C; July mean maximum temperature is 26.5°C. Mean annual precipitation is 133 cm with 80 percent of this precipitation occurring between 1 October and 31 March (U.S. NOAA, 1974).

Geology. The Nisqually Delta is located in the Puget Trough, a broad structural and topographic depression formed at the time of the final uplift of the present-day Cascade and Coast Range Mountains, 11 million years ago. Repeated glaciation of this area over the past two million years has resulted in the accumulation of large amounts of lacustrine and outwash sediments over the bedrock, as well as a deepening of the northern part of the Trough. Since the last glaciation (the Vashon Stade, 14,000 years ago), the Nisqually River, originating on Mount Rainier, has cut a deep valley into its floodplain. The formation of the present-day delta began about 6000 years ago when sea level attained its present position. During this time the delta advanced northward a distance of at least 2.4 km. It appears to be composed of alternating layers of sand, silt, and clay to a depth of about 42 m (The Nisqually Delta, 1970). Present-day surface sediments are typically black, medium to fine sands. At the present time the delta is thought to be at or near a state of dynamic equilibrium, neither advancing nor retreating (Brundage, 1960).

Description. The Nisqually salt marsh is made up of broad, relatively level, vegetated areas separated by wide drainage channels. These channels were formed, prior to diking, by distributaries of the Nisqually River. Each vegetated area is further dissected by a complex system of winding sloughs (drainage channels) which empty into the main channels and form the intricate drainage patterns characteristic of salt marshes. In the higher, relatively flat parts of the marsh, drainage is restricted to well-developed sloughs up to 2 m in depth. In the lower, gradually sloping vegetated areas, a more diffuse drainage pattern creates a hummocky topography.

Closely associated with the drainage of the salt marsh are salt pans, circular or semi-circular depressions which frequently contain standing water. Four types of salt pan, formed in various ways by vegetation (Chapman, 1964), are present on the

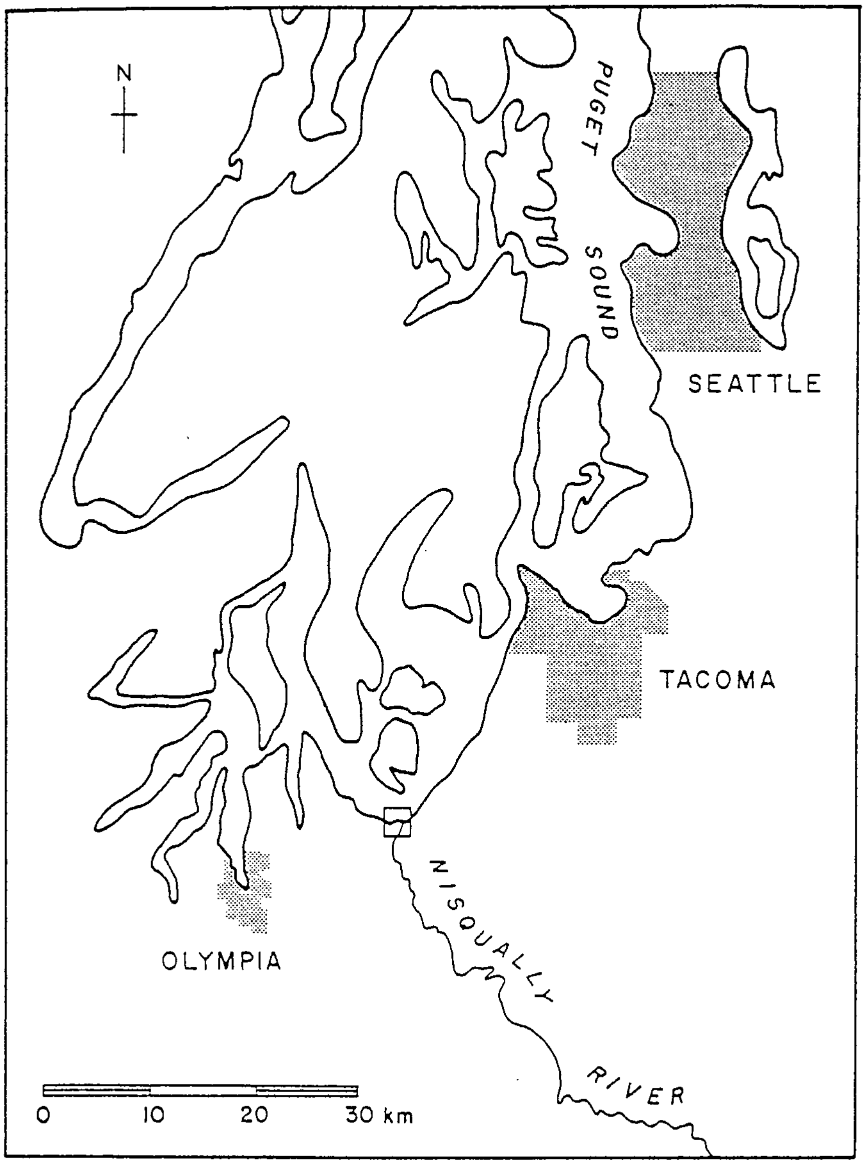

Figure 1. Location of the Nisqually River delta and salt marsh on southern Puget Sound, Washington.

Nisqually marsh. In addition to these we have observed another type of salt pan, commonly inhabited by burrowing Crustacea, which appears to be formed independent of vegetation.

Two types of transition from salt marsh vegetation to unvegetated mudflat characterize the Nisqually salt marsh. The first of these is the gradual slope, characteristic of areas where there is an accretion of sediment or where erosion from upland drainage is not great. The second type of transition is the steep erosion bank. This feature is found where erosion from upland drainage is greater than accretion; it is restricted to the banks of the Nisqually River and McAllister Creek and areas under the influence of littoral currents.

The Nisqually salt marsh is a complex mosaic of plant communities. The distribution of plant species is determined to a large extent by tidal inundation and factors related to this phenomenon: salinity, water table, nutrient cycling, and aeration. Proximity to fresh water is also an important factor. The zonation of salt marsh vegetation can be traced from the banks of the Nisqually River to the areas farthest from the river's influence. Closest to the river are large expanses of meadow dominated by tussock grasses. In areas bordering the major sloughs near the river are pure stands of sedge. Still farther from the river, there is a transition to zones typified by low-growing forbs and grasses. The lowest elevations throughout the marsh are sparsely vegetated by pioneer species.

Methods

Plant associations. Our study was conducted between April and October 1975. In July, when nearly all species were either flowering or beginning to flower, we recorded species present and estimated their percent areal cover in a total of 138 quadrats along 12 transects placed perpendicular to observed variation in vegetation zonation and apparent salinity and elevation-inundation gradients. The quadrats were placed at 30-m intervals along the transects except in one area of broad zonation in which the quadrat interval was 60 m.

We analyzed the data using an indirect polar ordination method (Bray and Curtis, 1957) based on a species importance value, the cover class midpoint of each species in each quadrat. Four BASIC computer programs were written to perform the required ordination calculations. Co-ordinates for each quadrat were plotted on a two-dimensional graph. Groupings of similar quadrats on the graph were interpreted as representing distinct plant associations.

Primary productivity. Because it was necessary to initiate productivity sampling prior to the sampling conducted to obtain plant association data, sampling sites were located, on the basis of our reconnaissance, in what appeared to be distinct plant communities. Two communities were sampled in May; subsequent sampling at monthly intervals from June through October included eight communities. At each sampling period, three 0.25-m^2 quadrats were subjectively placed in areas representative of each community. All vegetation, both living and standing dead, was clipped to the ground and brought back to the laboratory. Successive samples avoided plots previously clipped. Living and dead material were separated in each quadrat sample, and living vegetation was sorted by species. All material was oven-dried at 100°C for 48 hours, then weighed.

Net aerial primary productivity was estimated by summing peak biomass of individual species in each association and, when possible, biomass lost to death and shedding. No attempt was made to estimate below-ground productivity or biomass lost to tidal export and herbivory. Peak species' biomass was used instead of peak standing crop because species reach peak growth at different times during the growing season. Peak standing crop omits a part of the contribution to annual productivity made by plants maturing before or after peak standing crop is reached and yields a lower estimate (Eilers, 1975). Weights from each of the three quadrat samples taken monthly

TABLE 1. Association table. Average cover (COV) and frequency (FRE) for each of the 24 species characterizing 10 plant associations on the Nisqually salt marsh. (SPMA—Spergularia marina; SAVI—Salicornia virginica; DISP—Distichlis spicata; JACA—Jaumea carnosa; CALY—Carex lyngbyei; JUBA—Juncus balticus; DECE—Deschampsia cespitosa; FERU—Festuca rubra). (+ indicates less than one percent).

ASSOCIATIONS	SPMA		SAVI		DISP		DISP-SAVI		JACA-DISP		CALY-DISP		DISP-JUBA		CALY-DECE		FERU-CALY		CALY	
No. quadrals	6		2		9		27		34		23		4		13		11		2	
SPECIES	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE	COV	FRE
Spergularia marina	97.5	100																		
Salicornia virginica			45.8	100	+	33	37.9	85	18.1	97	4.3	39								
Agrostis alba			8.5	50			+	3	+	3	1.6	4					+	9		
Distichlis spicata					76.3	100	62.6	100	33.9	100	34.6	91	78.9	100	11.0	46	3.3	27		
Triglochin maritimum					+	11	12.2	37	16.4	88	26.8	87	1.8	25	10.0	46	6.6	54		
Carex lyngbyei					+	11	+	7	2.1	30	40.1	100	9.9	50	18.6	85	15.8	64		
Grindelia integrifolia					+	11	5.8	18	8.4	70	10.9	78	+	25	29.0	100	17.9	73	97.5	100
Jaumea carnosa					+	11	9.6	44	42.9	97	14.8	65	+	25	+	8				
Atriplex patula					+	11	+	37	+	70	+	22								
Spergularia canadensis							+	18	+	33										
Cuscuta salina							+	4	6.5	70	+	13								
Glaux maritima							+	7	4.0	70	5.8	96	1.2	50	4.6	77	3.7	64		
Plantago maritima									19.5	79	13.0	65			+	8	+	9		
Juncus balticus									1.1	3	+	4	47.6	100	7.4	62	16.1	54		
Stellaria humifusa									+	9	2.2	61			+	15	+	9		
Hordeum jubatum									+	6	+	4	9.2	25	+	8				
Potentilla pacifica											20.7	74	1.2	50	22.6	92	8.0	82		
Deschampsia cespitosa											+	13	3.5	50	25.4	100	15.5	91		
Hordeum brachyantherum													+	25			+	18		
Lilaeopsis occidentalis													3.4	15						
Aster eatonii													+	8						
Festuca rubra																	11.8	64		
Trifolium wormskjoldii																	82.8	100		
Galium triflorum																	1.5	9		
																	3.4	9		

in each association were averaged to yield one monthly value for each species in each association.

The method used to determine biomass lost to death and shedding was not the same for all associations. Since the dates of maximum production for different species and the effects of tidal inundation vary from one association to another, estimates were based on field observations and data collected for each association.

Results and Discussion

Plant associations. A total of twelve plant associations was identified. Two associations, the *Deschampsia cespitosa-Juncus balticus* association and the *Distichlis spicata-Carex lyngbyei* association, were recognized during the field mapping process. Ordination analysis resulted in the definition of ten plant associations, confirming the eight communities included in our productivity sampling, and revealing two additional associations not recognized during our initial reconnaissance. A list of these ten associations,

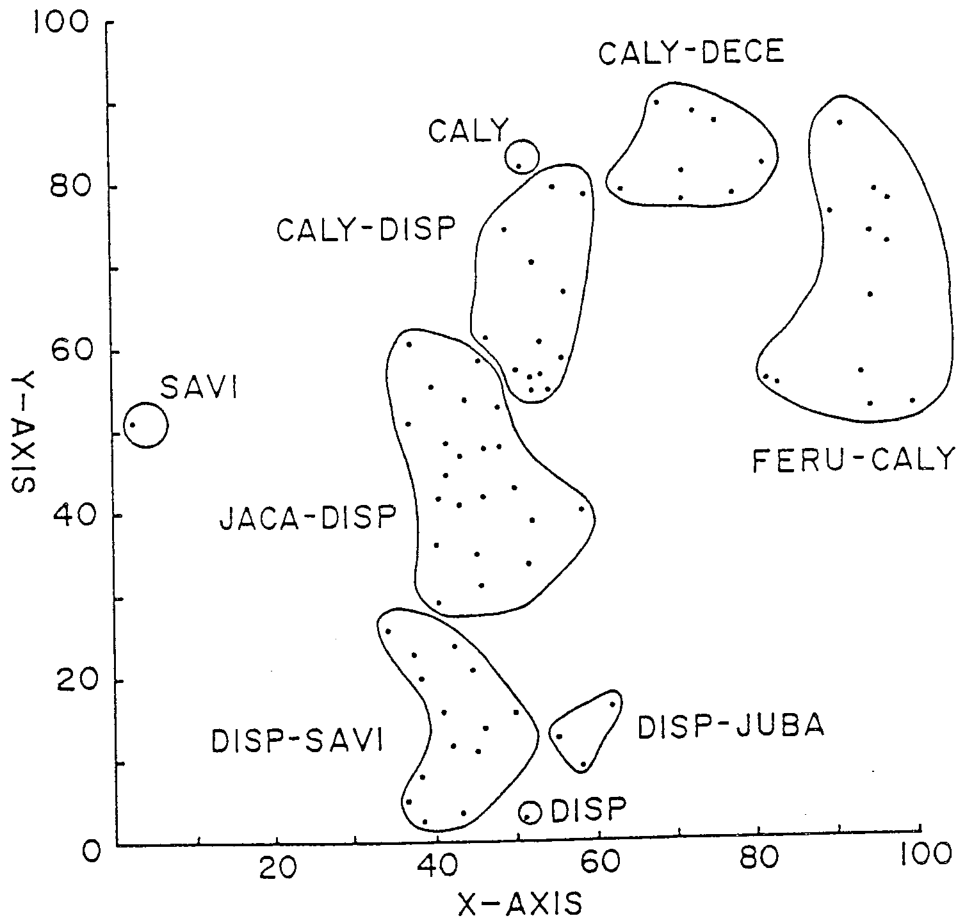

Figure 2. Plotted locations of individual quadrats as determined by computer-aided indirect polar ordination. Distance between points is a function of floristic similarity: the closer the points, the greater the similarity in species composition in terms of species present and their percent areal cover. (For definition of abbreviations, see Table 1.)

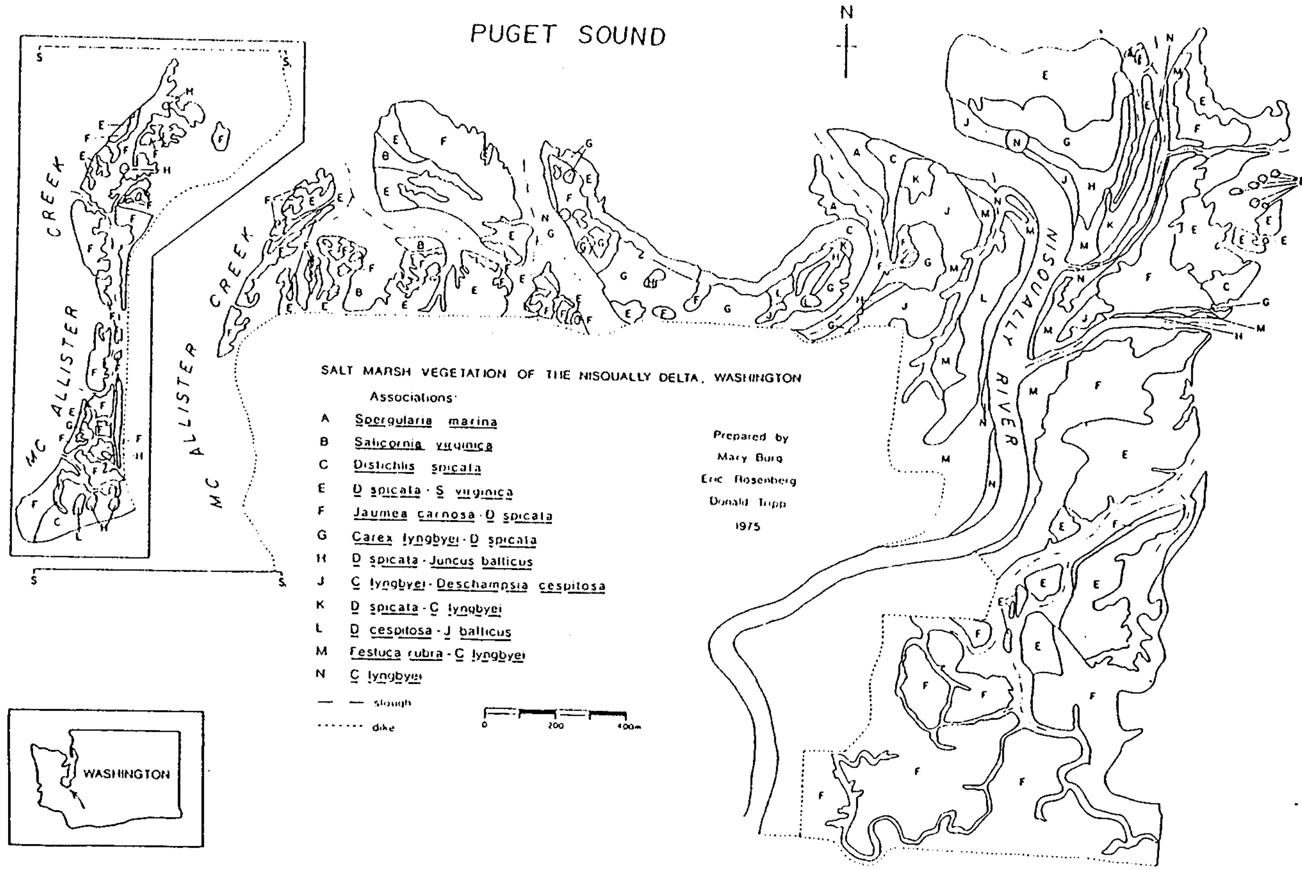

Figure 3. Vegetation map showing the location and extent of the 12 plant associations of the Nisqually Delta salt marsh.

including cover and frequency data for their component species, is given in Table 1. Nomenclature is after Hitchcock and Cronquist (1973).

The quadrat distribution of nine associations is shown on the ordination diagram, Figure 2. The *Spergularia marina* association is not plotted. It is composed of a single species which exhibits a narrow ecological tolerance and which is not present in any other association. Quadrats falling within this association appear totally dissimilar to every other quadrat and cause the remaining quadrats to clump at the opposite end of the axis, complicating further ordination. It was necessary to remove the *S. marina* quadrats before ordination could be satisfactorily completed.

Following is a brief description of each of the twelve plant associations recognized on the Nisqually salt marsh. A vegetation map showing the extent and location of these associations is presented in Figure 3.

1. The *Spergularia marina* association occurs on the gradually sloping transition zones at the lowest elevations on the marsh. *S. marina*, an annual, is the sole species constituting this association. It is a pioneer species which colonizes the mudflat and occurs in no other association. The largest stands are found at the mouth of the Nisqually River. Within the stands, it grows most vigorously adjacent to drainage sloughs and salt pans.

2. The *Salicornia virginica* association is also found at low elevations. Its thickly matted vegetation grows in patches in areas characterized by a diffuse drainage pattern and hummocky topography. It appears to be restricted to a well-drained, well-aerated substrate and is commonly found in soils inhabited by burrowing Crustacea. At the mouth of the river where invertebrate burrows are uncommon, the occurrence of *S. virginica* decreases markedly. Reproduction of this species is largely vegetative, as evidenced by its abundant rhizomes and its patchy growth habit.

3. The *Distichlis spicata* association is confined to low elevations where fresh water influence is present and where decreased aeration of the substrate excludes *S. virginica*. *D. spicata* is the dominant species with the occasional occurrence of *S. virginica* and *Triglochin maritimum*. *D. spicata* has a wide range of ecological tolerance. Capable of reproducing vegetatively or by seed, it is present in nearly every association on the marsh.

4. The *Distichlis spicata-Salicornia virginica* association occupies a habitat intermediate to those characteristic of the *S. virginica* and the *D. spicata* associations. It occurs at low elevations and, in some cases, extends to the margin of the bare mudflat. Vegetation cover is frequently interrupted by the shallow drainage sloughs of the gradually sloping transition zones. *D. spicata* is the dominant, followed by *S. virginica*. A distinguishing feature of this association is the presence of *T. maritimum* in its tussock growth form. Reproduction appears to be predominantly vegetative, though all these species are capable of reproduction by seed. In the spring and summer, tussocks of *T. maritimum* are often draped with mats of brown and green algae.

5. A low, dense, continuous vegetation cover typifies the *Jaumea carnosa-Distichlis spicata* association. It occurs on relatively level areas of the marsh. Its physical appearance is marked by well-developed drainage sloughs up to 1 m deep and the presence of salt pans. A total of 15 species occurs in this association. The characteristic species in order of dominance are *J. carnosa*, *D. spicata*, *Plantago maritima*, *T. maritimum*, *Grindelia integrifolia*, *Cuscuta salina*, and *Glaux maritima*. A conspicuous feature of

this association is the concentration of *G. integrifolia* along the tops of slough banks. This species appears to thrive in well-drained areas, and its occurrence is associated with an increase in *S. virginica.* The parasitic spermatophyte *C. salina* is most often found entwining *S. virginica* and *P. maritima.*

6. Dense stands of the *Carex lyngbyei-Distichlis spicata* association occur in the less saline areas of the marsh and are frequently found bordering the upper margins of the *J. carnosa-D. spicata* association. Closer to the Nisqually River, the *C. lyngbyei-D. spicata* association replaces the *J. carnosa-D. spicata* association. The physical appearance is similar to that of the *J. carnosa-D. spicata* association with the addition of *C. lyngbyei* evenly distributed among the other species. Sixteen species are found in this association, the most abundant being *C. lyngbyei, D. spicata, T. maritimum, Potentilla pacifica, J. carnosa, P. maritima*, and *G. integrifolia.*

7. Along the gradually sloping banks of the major sloughs, pure stands of the sedge *Carex lyngbyei* form one of the most interesting associations on the marsh. In this association a tall growth form of *C. lyngbyei* begins its growing season in the fall after most of the previous year's aerial growth has been exported by the tides. At this time, shoots sprout from the rhizomes, remain green all winter, and by May are vigorous and up to 1 m in height. The plants flower in late May and reach a maximum height of 1.5 m by July. Where it occurs in multi-species associations, *C. lyngbyei* seldom exceeds a height of 0.5 m.

Eilers (1975) reported two phases of *C. lyngbyei*, both occurring in pure stands on West Island Marsh in Nehalem Bay, Oregon. One phase, a short growth form, occurs at the lowest elevations (0.77-2.06 m above MLLW). The second phase, a tall growth form (1.8 m or more), grows along sloping banks at elevations between 1.67 and 2.25 m above MLLW. Eilers also observed that *C. lyngbyei* exhibits a slower growth rate in multi-species communities.

8. The *Distichlis spicata-Carex lyngbyei* association is found at low elevations near the Nisqually River. Its lower margins are bordered by the *C. lyngbyei* association or the *D. spicata* association while its upper margins merge with tussock grass meadow vegetation. *D. spicata* and the short growth form of *C. lyngbyei* are co-dominants with a minimal presence of subordinate species. The appearance of this association, both in the field and on aerial photographs, is sufficiently different to distinguish it from any other association on the marsh.

9. The *Distichlis spicata-Juncus balticus* association occurs throughout the salt marsh. In areas closest to the Nisqually River it occurs in bands, bordered on its lower margins by the *C. lyngbyei-D. spicata* association and on its upper margins by the *C. lyngbyei-D. cespitosa* and *Festuca rubra-C. lyngbyei* associations. Farther from the influence of the river, this association occurs in patches up to 50 m in diameter. These patches are surrounded by the *C. lyngbyei-D. spicata* and *J. carnosa-D. spicata* associations. The association is dominated by *D. spicata* and *J. balticus*, followed by *C. lyngbyei* and *Hordeum jubatum*, with minimal amounts of *T. maritimum, P. pacifica* and *G. maritima.*

10. The *Carex lyngbyei-Deschampsia cespitosa* association appears as an area of thick, uniform vegetation cover cut by sloughs up to 2 m deep. The appearance of the area is dominated by the tall tussock grass, *D. cespitosa. C. lyngbyei* and *D. cespitosa*

are co-dominants occurring with *P. pacifica*, *T. maritimum*, *Agrostis alba*, *D. spicata*, *J. balticus*, and *G. maritima*.

11. The *Deschampsia cespitosa-Juncus balticus* association occupies an intermediate position between the *C. lyngbyei-D. cespitosa* and *Festuca rubra-C. lyngbyei* associations. The species composition and the physical characteristics of this association are similar to those of the *C. lyngbyei-D. cespitosa* association. However, the marked increase in the salt rush *J. balticus* and the decrease in *C. lyngbyei* warrants a distinction between these associations.

12. The *Festuca rubra-Carex lyngbyei* association is restricted to the highest areas immediately adjacent to the Nisqually River and its distributaries. The characteristic species of this association are *F. rubra*, which grows in thick tussocks, *C. lyngbyei*, *J. balticus*, *D. cespitosa*, *T. maritimum*, *Aster eatonii*, and *P. pacifica*. This association is bordered on its lower margins by the *C. lyngbyei-D. cespitosa* association. When located along major sloughs, its lower margins are bordered by the *C. lyngbyei* association.

Water salinity and elevation-inundation appear to be the two significant environmental gradients influencing zonation of vegetation on the Nisqually salt marsh. Aerial photographs and surface observations indicate that there is a strong westward current at the mouth of the Nisqually River. It is apparent from the map (Fig. 3) that this westward flow of fresh water influences distribution in relation to the above gradients. On the west side of the river, associations in which fresh water influence is significant (A,C,G,H,J,K,L,M,N on the map) generally cover broad areas; associations which are more salt tolerant (B,E,F) are located beyond these, far from the banks and mouth of the river. On the east side of the river, most of the associations greatly influenced by fresh water are restricted to narrow bands along the banks of the river and its major distributaries; the more salt tolerant associations are again located beyond them but much closer to the river than they are on the west side.

From areas near the river to areas farthest from the river's influence, widely different associations occur at identical elevations. For example, on the west side of the marsh along McAllister Creek (which has a negligible diluting effect), elevations as high as 4.8 m above MLLW are occupied by the *J. carnosa-D. spicata* association which is composed of species with high salt tolerances. At the same elevation but closer to the Nisqually River is found the *F. rubra-C. lyngbyei* association, composed of species less tolerant of salinity. These patterns of distribution indicate that the degree of fresh water influence may determine the presence or absence of an association while elevation-inundation determines the vertical distribution of associations within the boundaries set by salinity.

Away from the river's influence, a typical sequence of zonation begins with stands of the *S. virginica* and the *D. spicata-S. virginica* associations adjacent to the mudflats. These stands give way at higher elevations to the *J. carnosa-D. spicata* association with scattered patches of the *D. spicata-J. balticus* association.

At the mouth of the river where salinity is greatly reduced, discontinuous stands of the *S. marina* association occupy the lowest elevations. These stands are bordered on their upper margins by the *D. spicata* association. The occurrence of the *C. lyngbyei* association along the banks of the river and nearby sloughs also marks the decrease in salinity, although the distribution of this association may also be a function of drainage (Eilers, 1975). At intermediate elevations, stands of the *C. lyngbyei-D. spicata* association are extensive just west of the river mouth and decrease in size and occurrence farther to the west. The highest areas closest to the river are characterized by the *C. lyngbyei-D. cespitosa, D. cespitosa-J. balticus*, and *F. rubra-C. lyngbyei* associations. The individual species which best mark the decrease in salinity by the influence of the Nisqually River are *C. lyngbyei, D. cespitosa, F. rubra, P. pacifica*, and *A. eatonii.*

Primary productivity. Annual net productivity was estimated for eight plant associations: *S. marina, S. virginica, D. spicata-S. virginica, J. carnosa-D. spicata, C. lyngbyei-D. spicata, D. spicata-J. balticus, F. rubra-C. lyngbyei*, and *C. lyngbyei.* Individual species' peak biomass and monthly totals of living and dead material for these associations are presented in Tables 2 and 3, respectively. Estimates of annual net productivity, based on these data, are summarized in Table 4.

Annual net productivity of the *S. marina* association is 90 g dry weight/m^2. This value was obtained from maximum biomass alone. Since this association occurs in the pioneer zone, a salt marsh habitat which is inundated twice daily throughout the year, plant material that dies can be removed by tidal waters within a day. As a result we found no dead plant material in the samples. Fluctuations in monthly samples probably reflect quadrat placement and the scattered growth of individual plants within this association.

The annual net productivity of the *S. virginica* association is 730 g dry weight/m^2. This value was derived from maximum biomass. We did not differentiate between living and dead material since many apparently dead plants (those without leaves) were found to have green vascular tissue. Leaves of *S. virginica* are easily broken off of living plants, and it is likely that the twice daily tides removed this material.

Annual net productivity estimates for the *D. spicata-S. virginica* and the *J. carnosa-D. spicata* associations are 952 g dry weight/m^2 and 800 g dry weight/m^2, respectively. Estimates for both associations were made by computing the difference between values for dead material found in July and August samples and adding this amount to the peak species' biomass total. Peak standing crop for both associations was reached in August; the lowest values for dead material occurred in July. We assumed that any increase in dead material after July was derived from the current year's production.

Annual net productivity for the *C. lyngbyei-D. spicata*, the *D. spicata-J. balticus*, and the *F. rubra-C. lyngbyei* associations is estimated at 908 g dry weight/m^2, 558 g dry weight/m^2, and 1086 g dry weight/m^2, respectively. Because these associations are found at higher elevations where the effects of tidal action are reduced, dead material remains on site for long periods of time. This point is especially true of the *F. rubra-C. lyngbyei* association where, except in the month of July, the amount of dead material present was always greater than that of live material. Since we were unable to determine what proportion of dead material could be attributed to the current growing season, estimates of these associations are based on peak species' biomass alone and are necessarily low.

The annual net productivity of the *C. lyngbyei* association is 1390 g dry weight/m^2. This value was determined by summing weights of living and dead material in July, the time of peak biomass production. In this association all of the previous year's

TABLE 2. Individual species' peak biomass. Shows peak productivity values in dry weight g/m² for each species in each of the eight associations sampled. (M) = month during which individual species reached peak biomass production. (For definition of abbreviations, see Table 1).

ASSOCIATIONS	SPMA		SAVI		DISP-SAVI		JACA-DISP		CALY-DISP		DISP-JUBA		FERU-CALY		CALY	
SPECIES	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)	g/m²	(M)
Spergularia marina	90	(10)														
Salicornia virginica			730	(8)	672	(8)	100	(7)	100	(10)	8	(6)				
Agrostis alba							4	(7)								
Distichlis spicata					270	(7)	68	(8)	110	(8)	52	(7)	66	(7)		
Triglochin maritimum							140	(7)	126	(6)	108	(6)	154	(7)		
Carex lyngbyei							2	(6)	332	(7)			50	(7)	1180	(7)
Grindelia integrifolia											4	(6)				
Jaumea carnosa							370	(8)	116	(9)	34	(7)				
Atriplex patula							2	(7)			2	(6)				
Spergularia canadensis							4	(8)								
Glaux maritima							4	(6)	8	(7)	4	(6)	12	(8)		
Plantago maritima							96	(6)	26	(8)			2	(7)		
Juncus balticus											330	(8)	80	(9)		
Stellaria humifusa									2	(6)			2	(6)		
Hordeum jubatum									2	(6)			14	(6)		
Potentilla pacifica									86	(7)	16	(8)	40	(7)		
Deschampsia cespitosa													344	(10)		
Festuca rubra													322	(6)		
TOTALS	90		730		942		790		908		558		1086		1180	

growth is removed by the tides during the fall of the same year, so any dead material found in July is of the current year's production.

Eilers (1975) estimated annual net productivity for ten of the eleven salt marsh communities on West Island Marsh using the sum of individual species' peak biomass and biomass lost to death and shedding during the current growing season. He reported average net productivity values ranging from 518 g to 1936 g dry weight/m^2. The most productive was the high elevation *Aster-Potentilla-Oenanthe* community which contributed 20 percent of total marsh productivity from 14.7 percent of the

TABLE 3. Average dry weights of live and dead material from the eight associations sampled monthly between May and October. (For definition of abbreviations, see Table 1.)

ASSOCIATIONS	MAY	JUN	JUL	AUG	SEP	OCT
	g/m^2	g/m^2	g/m^2	g/m^2	g/m^2	g/m^2
SPMA						
Live	—	20	20	60	40	90
Dead	—	–0–	–0–	–0–	–0–	–0–
SAVI						
Live	120	170	240	730	530	400
Dead	–0–	–0–	–0–	–0–	–0–	–0–
DISP-SAVI						
Live	120	310	630	920	770	440
Dead	380	310	260	270	260	340
JACA-DISP						
Live	—	410	570	600	370	280
Dead	—	130	100	110	190	170
CALY-DISP						
Live	—	250	720	500	460	260
Dead	—	470	200	240	310	400
DISP-JUBA						
Live	—	470	460	390	280	90
Dead	—	260	210	300	230	330
FERU-CALY						
Live	—	640	560	630	400	360
Dead	—	870	460	840	460	620
CALY						
Live	—	750	1180	740	1020	10
Dead	—	270	210	–0–	–0–	110

TABLE 4. Summary of association and productivity data. Shows the area in hectares and the percentage of total marsh area of each of the twelve associations and annual net productivity in dry weight, total net production (area · productivity), and percentage of total marsh production for the eight associations sampled. (For definition of abbreviations, see Table 1.)

ASSOCIATIONS	AREA		ANNUAL NET PRODUCTIVITY		ANNUAL NET PRODUCTION	
	Total ha	% Total area	g/m^2	kg/ha	Total kg	% Total
SPMA	2.3	1%	90	900	2070	0.1%
SAVI	1.9	1	730	7300	13,870	0.9
DISP-SAVI	47.1	22	952	9520	448,392	26.8
JACA-DISP	86.0	39	800	8000	688,000	41.2
CALY-DISP	15.8	7	908	9080	143,464	8.6
DISP-JUBA	15.6	7	558	5580	87,048	5.2
FERU-CALY	16.2	7	1086	10,860	175,932	10.5
CALY	8.0	4	1390	13,900	111,200	6.7
DISP	8.2	4				
DISP-CALY	2.6	1				
DECE-JUBA	5.6	3				
CALY-DECE	8.9	4				

total area of the marsh. The estimated average net productivity of pure stands of the tall growth form of *C. lyngbyei* was 1746 g dry weight/m^2, a contribution of 12.2 percent to total productivity from an area covering 9.6 percent of the total area of West Island Marsh.

The total dry weight net production of the eight associations sampled on the Nisqually salt marsh is estimated to be 1670 metric tons produced over an area of 192.9 ha. The remaining four associations cover a total area of 25.3 ha. Net production and area of each association are listed in Table 4. These values provide a basis for comparing the contribution of each association to the total productivity of the marsh.

C. lyngbyei is the most productive of the associations sampled. It covers 8 ha, 4 percent of the total area of the marsh, and contributes 6.7 percent of total marsh production. The high elevation *F. rubra-C. lyngbyei* association is the second most productive association, covering 7 percent of the total area of the marsh and contributing 10.5 percent of the total production of the Nisqually salt marsh.

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